

Network Science and the Effects of Music Preference on Functional Brain Connectivity: From Beethoven to Eminem

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Abstract:

Most people choose to listen to music that they prefer or ‘like’ such as classical, country or rock. Previous research has focused on how different characteristics of music (i.e., classical versus country) affect the brain. Yet, when listening to preferred music—regardless of the type—people report they often experience personal thoughts and memories. To date, understanding how this occurs in the brain has remained elusive. Using network science methods, we evaluated differences in functional brain connectivity when individuals listened to complete songs. We show that a circuit important for internally-focused thoughts, known as the default mode network, was most connected when listening to preferred music. We also show that listening to a favorite song alters the connectivity between auditory brain areas and the hippocampus, a region responsible for memory and social emotion consolidation. Given that musical preferences are uniquely individualized phenomena and that music can vary in acoustic complexity and the presence or absence of lyrics, the consistency of our results was unexpected. These findings may explain why comparable emotional and mental states can be experienced by people listening to music that differs as widely as Beethoven and Eminem. The neurobiological and neurorehabilitation implications of these results are discussed.

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Network Science and the Effects of Music Preference on Functional Brain Connectivity: From Beethoven to Eminem

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Most people choose to listen to music that they prefer or ‘like’ such as classical, country or rock. Previous research has focused on how different characteristics of music (i.e., classical versus country) affect the brain. Yet, when listening to preferred music—regardless of the type—people report they often experience personal thoughts and memories. To date, understanding how this occurs in the brain has remained elusive. Using network science methods, we evaluated differences in functional brain connectivity when individuals listened to complete songs. We show that a circuit important for internally-focused thoughts, known as the default mode network, was most connected when listening to preferred music. We also show that listening to a favorite song alters the connectivity between auditory brain areas and the hippocampus, a region responsible for memory and social emotion consolidation. Given that musical preferences are uniquely individualized phenomena and that music can vary in acoustic complexity and the presence or absence of lyrics, the consistency of our results was unexpected. These findings may explain why comparable emotional and mental states can be experienced by people listening to music that differs as widely as Beethoven and Eminem. The neurobiological and neurorehabilitation implications of these results are discussed.

Listening to music affects an intricate set of complex processing systems in the brain¹, such as systems associated with sensory-motor processing as well as functional elements implicated in memory, cognition and emotion or mood fluctuation^{2–5}. Listening to music often connects thoughts and emotions and, therefore, is associated with questions surrounding consciousness and “Theory of Mind” (the ability to understand the intentions and emotional state of others)^{6–8}. However, little is understood about how listening to music affects the brain^{9–11}.

One of the most challenging neuroscientific questions surrounding the phenomenon of music preferences is how listening to different types of music can connect the same brain systems (i.e. similarly experienced circuits in the brain) associated with thoughts and memories¹².

People primarily choose to listen to music that they like^{13,14}, such as country, rock or classical. When listening to strongly preferred music, people report they often experience deeply personal, often unsolicited and emotionally-laden, thoughts and memories¹⁵. Listeners describe that the phenomenon of self-referential thoughts and memories can be triggered by different types of music and the presence or absence of lyrics¹⁶. However, music listening preferences are highly individualized and culturally diverse^{17,18}, and different types of music can vary substantially in their melodic and harmonic features and rhythmic complexity¹⁹. What remains unanswered is why listening to different types of music can generate similar experiences within the brain. To date, it remains unclear how listening to different types of music can generate these types of similar brain experiences across various individuals¹⁸.

Network science is a rapidly emerging and promising analysis method for investigating complex systems in terms of their elements and the relationships and interactions between the network elements^{20–22}. The recent advent of studying the brain as a complex system offers a fuller understanding of brain organization and function^{23,24}. We applied network science techniques to determine whether certain brain patterns of functional connectivity might be associated with an individual’s musical preferences. Network science methodological advances offered us the opportunity to simulate more real-world music listening experiences for our participants²⁰. Similar to recent efforts to evaluate ecological aspects of music listening^{25–29}, a specific characteristic of this investigation was that our functional imaging data were collected while people listened to complete songs

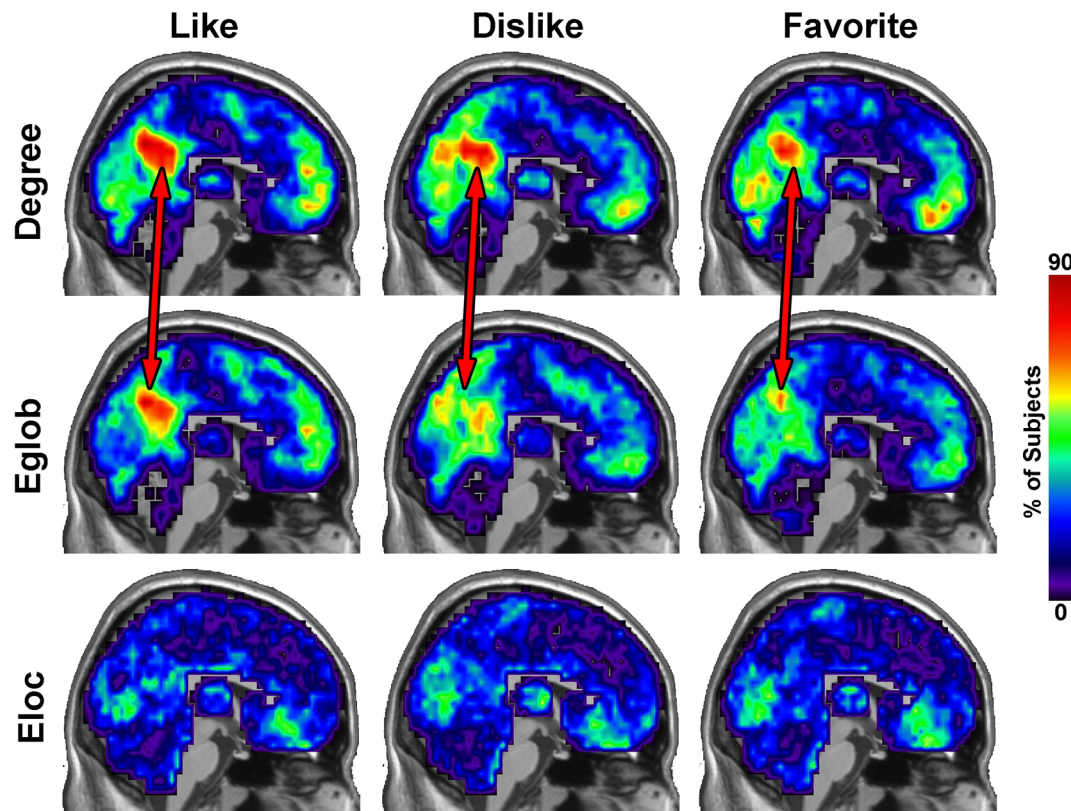


Figure 1 | Demonstration of degree, global efficiency and local efficiency in the precuneus. The precuneus exhibited consistent high degree across participants regardless of music preference. Despite being a high degree hub, compared to the Like condition, the precuneus showed relatively lower global efficiency in the Dislike and Favorite conditions. The precuneus has relatively low local efficiency, and there was no difference across the 3 conditions. The scale depicts the percentage of subjects that has a top 20% node in each area for all three network statistics.

from the following genres: classical, country, rap, rock, Chinese opera, and a participant's pre-reported favorite song. As an investigation into the under-explored area of musical enjoyment, we applied network science techniques to brain imaging data gathered while people listened to entire songs in an uninterrupted fashion. Our first analyses sought to identify functional connectivity changes based on the genre or 'type' of music¹⁹. Here we investigated how listening to preferred music, naturally associated with introspective thought, emotion, and memory, affected functional brain connectivity patterns compared to music that was not preferred. The fact that comparisons were based on individual listening preferences meant that various preferential genres were presented. In order to differentiate between music preference and potential brain networks responding to an individual's personal favorite song, we also evaluated brain responses to each participant's pre-reported favorite song as a separate condition. From this, we were able to determine brain connectivity during the preferred, non-preferred, and favorite conditions.

Results

Music Preference and Brain Networks. We evaluated brain networks from functional magnetic resonance imaging (fMRI) data collected while 21 people listened to five iconic musical selections from different pre-chosen genres and their personal favorite song that was self-reported during their pre-study screening. During the scanning session, participants rated each of the musical selections using a sliding scale to indicate how much they liked the song (see Methods). Whole-brain voxel-based functional networks were created for each participant's three reported conditions: most preferred song, least preferred song (i.e., 'liked' and 'disliked'), and a pre-reported favorite song. Brain networks were created using each

imaging voxel as a network node, and correlation analyses identified network connections. The cross-correlation matrix was thresholded to yield a binary network with a 1 indicating a connection between voxels, or nodes, and a 0 indicating the absence of a connection. Our results show the consistency of brain networks^{20,30} across the participants based on the three reported conditions. Here, we focus on four basic network science statistics: degree, global efficiency, local efficiency and modularity or "community structure" (for a detailed explanation see Methods and Supporting Information).

Default Mode Network and Music Listening. A fundamental measurement of brain connectivity is degree (K), which represents the number of edges or functional links for each node within the brain network²⁰. Our results show that across study participants high degree nodes, or hubs, were located in the default mode network (DMN)³¹ generally, and within the precuneus particularly, regardless of song preference (Figure 1, arrows). The DMN is known to support functional brain states, such as the reprocessing of memories and introspection (i.e. self-referential thoughts)³². Statistical comparisons within the precuneus showed that degree did not differ significantly across conditions (mean degree \pm S.D: Like = 53.94 ± 0.39 ; Dislike = 54.06 ± 0.33 ; Favorite = 53.95 ± 0.48 ; $F(1, 20) = 1.10$, $p = 0.34$); however, the precuneus was a hub relative to the rest of the brain.

Global Brain Efficiency and Music Preference. Despite the precuneus being a hub regardless of preference, there were significant differences in global efficiency in the precuneus for the different conditions. Global efficiency is a surrogate measure of path length, or the number of steps connecting a node to the rest of the functional network nodes. Higher global efficiency indicates fewer steps to

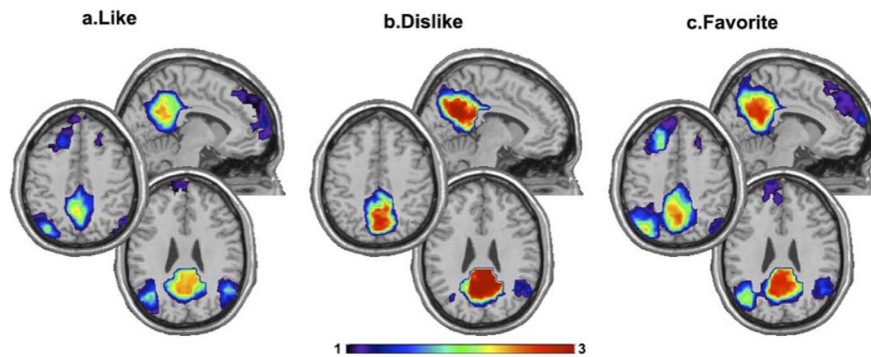


Figure 2 | Demonstration that there are differences in the structure of precuneus community within the default mode network depending on music preference. In the Liked and Favorite condition, the precuneus was consistently interconnected with lateral parietal and medial prefrontal cortex (a and c). When the music was disliked, the precuneus was relatively isolated from the rest of the default mode network (b.). Color indicates the consistency of community structure for each voxel across subjects as assessed using scaled inclusivity (see Methods and Supporting Information).

reach the rest of the network and may be associated with an increased ability to rapidly combine information across distributed brain regions. Mean global efficiency \pm S.D in the precuneus was: Like = 0.206 ± 0.018 ; Dislike = 0.194 ± 0.018 ; Favorite = 0.203 ± 0.017 ; $F(2, 17) = 3.58$, $p = 0.04$. Global efficiency was significantly higher in the precuneus during the Liked music condition compared to the Disliked condition ($p = .017$). There was no significant difference in global efficiency between the Liked music and the Favorite music condition ($p = .330$), nor between Favorite and Disliked music ($p = .132$). Figure 1 pictorially depicts the consistency of the brain location for global efficiency (Eglob) across subjects. Comparisons of local efficiency, a measure of local clustering, showed no significant differences between the 3 conditions. Local efficiency values were 0.721 for Like, 0.723 for Dislike, and 0.717 for Favorite, with no p -values less than 0.32.

It is quite common for network nodes that have high degree to also have high global efficiency. The fact that we found the precuneus to be a “hub” with high degree regardless of musical preference, but that there were significant differences in global efficiency between Liked and Disliked music, led to a more detailed exploration of precuneus connectivity. Given similar number of connections but different global efficiency indicates that there must be differences in the regions to which the precuneus is connected. A community structure analysis was performed to determine to which nodes the precuneus was most closely functionally connected during the Like, Dislike, and Favorite conditions. Community structure identifies the organization of the network by measuring those nodes that are more highly connected to each other than to other nodes in the brain network (thus forming a so-called functional neighborhood). Our results indicate that listening to liked or favorite music affected the community structure differently than disliked music (Figure 2). For details on the methodology, see Methods and Supporting Information.

Default Mode Community Structure Differences and Preferential Music. When listening to liked and favorite music, we found that the precuneus community included all regions of the DMN (i.e., precuneus, lateral parietal, and medial frontal cortices) (Figure 2a and c). However, the precuneus community was different when listening to the most disliked song. Specifically, when listening to disliked music, the precuneus dissociated from the medial frontal cortices and was connected primarily only to itself (Figure 2b). This was the most consistent finding in the community structure analysis. In a small portion of the study participants, the precuneus did belong to a community with the lateral parietal lobes as noted by the dark blue regions, but the data clearly demonstrated that the medial frontal portion of the DMN was isolated from the precuneus when listening to music that was disliked. Due to the comple-

xity and multivariate nature of community structure measures and the fact that the consistency metric, scaled inclusivity, yields a single value for the entire population, it is currently not possible to perform traditional hypothesis tests to statistically compare the conditions. However, we performed a *post-hoc* analysis to measure the connectivity between the precuneus and the remainder of the DMN. The results showed a significant ($p = 0.04$) increase in connectivity in the Like condition compared to the Dislike condition. There was no significant difference between Like and Favorite ($p = 0.08$) or between Dislike and Favorite ($p = 0.71$). Details of the analysis methods and specific results including the number of connections measured are presented in the Supporting Information.

Auditory Cortex and Preferential Music: Global Efficiency. Our second major investigation in this study involved the auditory cortex, not surprisingly, given the auditory-specific nature of this study. Figure 3 is analogous to Figure 1 in that we show degree, global efficiency, and local efficiency of the auditory cortex. As expected, auditory cortex in the superior temporal region is a hub for liked, disliked, and favorite music. Mean degree \pm S.D in auditory cortex was: Like = 88 ± 39 ; Dislike = 73 ± 48 ; Favorite = 76 ± 51 , and there were no significant differences between degree for the 3 conditions (Like vs. Dislike, $p = .09$; Like vs. Favorite, $p = .20$; Dislike vs. Favorite, $p = .78$). As degree and global efficiency are typically coupled, it was again surprising to find the significantly higher global efficiency in the auditory cortex when listening to the liked song compared to Dislike and Favorite (Like vs. Dislike, $p = .002$; Like vs. Favorite, $p = .016$; Dislike vs. Favorite, $p = .35$). Mean global efficiency \pm S.D in auditory cortex was: Like = 0.21 ± 0.02 ; Dislike = 0.19 ± 0.02 ; Favorite = 0.2 ± 0.02 . As observed in the precuneus, there was no significant difference in local efficiency between the three conditions and is not discussed further.

Community Structure and Favorite Music: Hippocampus and Memory. Given this dissociation between Eglob and degree in the auditory cortex, we again performed a community structure analysis to determine the auditory neighborhood. In the Like and Dislike conditions, the auditory cortex community included the hippocampi, a region recognized to be associated with memory consolidation (Figure 4a). However, in the Favorite condition, the hippocampus functionally separated from the auditory cortex, with the hippocampus becoming its own distinct community (Figure 4b). Although the consistency of the hippocampus was relatively low compared to auditory cortex, it clearly belonged to an isolated community in the Favorite condition. The auditory cortex had disengaged from the hippocampus despite the varied presence or absence of text (lyrics) and acoustic complexity of the personal favorite musical selections.

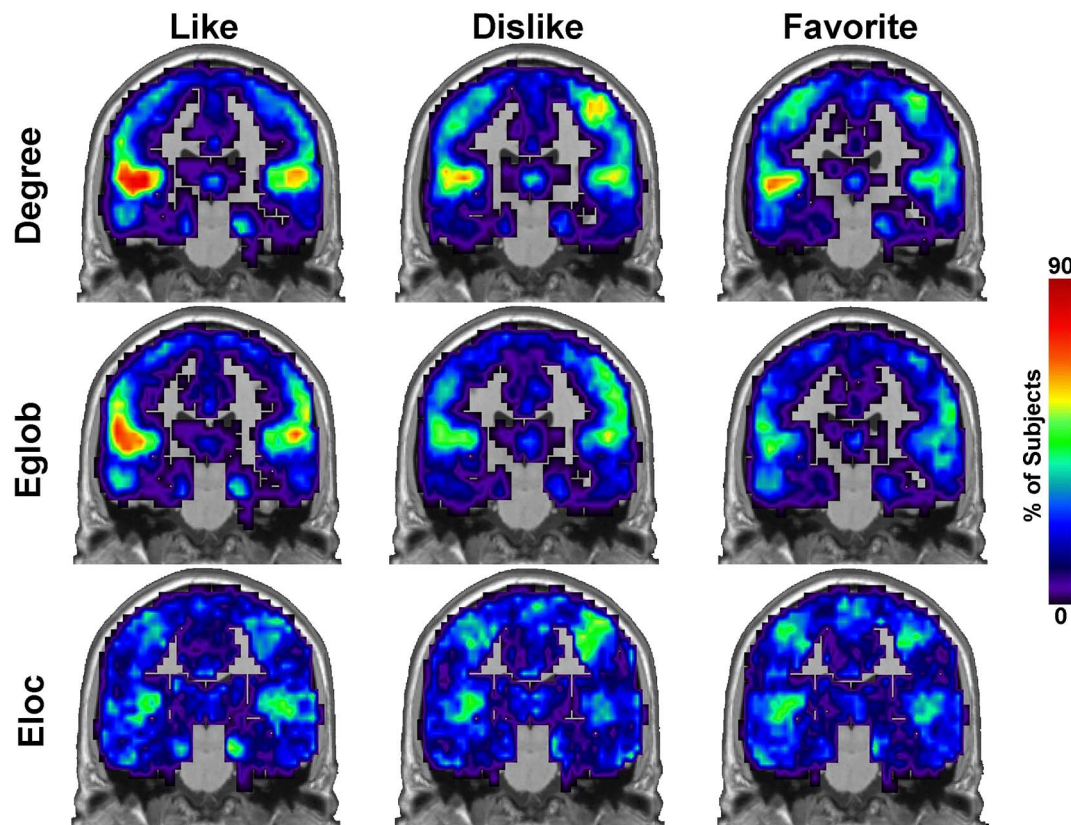


Figure 3 | Demonstration of degree, global efficiency, and local efficiency in the auditory cortex. The auditory cortex was a focus of high degree nodes in all three conditions. Although consistency is visually highest in the Liked condition, there was no significant difference across conditions. As observed in the precuneus, the global efficiency was consistently high in auditory cortex only in the Liked condition. Though there are obvious foci of high local efficiency nodes in the auditory cortex, the consistency was lower than other network statistics, and there was no difference across the 3 conditions. The scale depicts the percentage of subjects that has a top 20% node in each area for all three network statistics.

Discussion

We investigated the effects of music listening and preference on brain connectivity using network science techniques. To mimic as closely as possible a ‘real-world’ experience, complete songs rather than brief excerpts were used. Our previous analysis indicated that specific genres affected the connectivity of the auditory cortex differently¹⁹. Here we wanted to determine whether the application of network science techniques might reveal patterns of functional connectivity based on individual music listening preferences, including a pre-reported personal favorite song, regardless of the type of music¹⁹. Of particular interest to us were brain mechanisms responsible for self-reflective thought and socio-emotional memory^{33,34}. Previous analyses with fMRI and naturalistic listening have focused on brain network responses to specific components, such as timbral musical features and motifs, within a continuous musical excerpt^{27,29}. Here, we have shown that when listening to complete songs, there are consistent patterns of network connectivity that exist within the brain that are related to preference. Our findings reveal that liked, disliked, or favorite music dictates this functional connectivity, regardless of the type of music or the presence or absence of lyrics. The compatibility between our results and what music listeners frequently self-report in terms of neurobiology and neurorehabilitation are discussed below. We include directions for future research based on the current findings.

The default mode or resting-state network has been shown to support specific brain functions, such as self-referential thoughts, emotional perspectives (i.e., empathy), and levels of self-awareness^{32,35}. Described as functioning somewhat like a toggle switch between outwardly focused mind states and the internal or subjective sense of self, this network appears to include mind-wandering experiences

such as imagining the future, the discovering of new possibilities (hopes), and the affective significance of aspirations or dreams^{31,33,36}. The demonstrated high degree within the precuneus concurrent with high global efficiency provides preliminary support for the recruitment of other cognitive processing states when listening to music that is liked^{37,38}. Interestingly, these patterns were present regardless of the genre or lyrics. When listening to liked music, the consistency of the community structure within the default mode network suggests compatibility with the listener’s experiences of musically-driven introspection¹². We suggest that such connectivity might perhaps support neural processes associated with other aspects of cognition. Specifically, it appears that the default mode community structure results align with those self-referential or ‘mind-wandering’ type experiences people report when listening to their preferred music^{9,39}.

The high degree of connectivity found within the precuneus combined with the default mode network community structure results suggest that listening to music that is preferred influences these emotionally-laden experiences in the brain^{40,41}. Research is now showing that disruptions and abnormal connectivity within the default mode network may be related to a set of neurological challenges, such as autism, mild cognitive impairment, post-traumatic stress disorder, schizophrenia, and depression^{35,42,43}. This network has also been more recently implicated in the development of cognitive abilities such as divergent thinking and creativity^{33,44}. Based on these findings, it might be possible that listening to preferred music has the potential to engage such brain functions³³. This has specific implications for neurologic remediation (therapy), where music has been shown to have neurorehabilitation effects, such as improvements in executive function and emotional adjustments, as well as

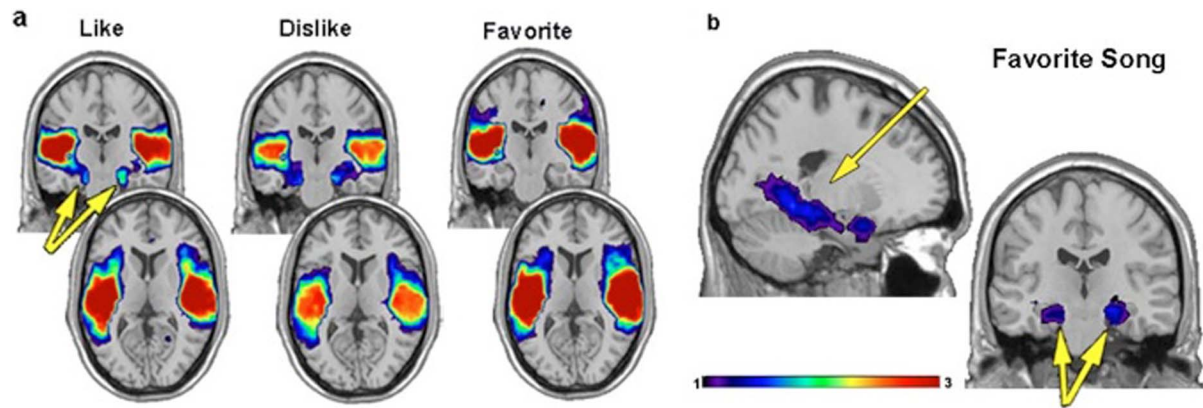


Figure 4 | Demonstration of differences in the community structure of the hippocampus and auditory cortex when listening to a favorite song. When listening to liked and disliked music, the hippocampi and auditory cortex were within the same community (a). The location of the hippocampi is indicated by the yellow arrows. When listening to a favorite song, the hippocampi were functionally separate from the auditory cortex and became an isolated community (b). Color indicates the consistency across subjects as assessed using scaled inclusivity (See Methods and Supporting Information).

lessening of anxiety and depression^{45,46}. Our results suggest that using each brain-injured person's preferred music might have a stronger effect than disliked music. Along with the findings from Alluri et al. who found a correlation of DMN activity with low-level timbral musical features²⁷, preferred music might better engage the DMN and thus affect the complex sensory-motor rhythmic integration that is observed with music neurorehabilitation.

Assessment of functional connectivity within the DMN, and particularly the precuneus, is emerging as a promising diagnostic measurement for patients suffering from disorders of consciousness (i.e., locked-in syndrome, vegetative state, and minimally conscious states)^{47–49}. Connectivity within the DMN is also emerging as a diagnostic measurement in autism⁵⁰, where understanding the inner representation of other people's affective state (i.e., empathy) is often compromised⁴¹. Our results suggest there may be some potential utility in listening to preferred music to optimally influence functional brain connectivity within this network^{47–49}. Clearly, future research is needed to more fully understand how music listening impacts these brain mechanisms.

Research on the structure and function of resting state and task-based connectivity have focused almost exclusively on static representations of connectivity patterns^{22,23}. However, recent results indicate that functional brain networks are highly plastic can be altered spontaneously and by exogenous stimulation⁵¹. In conjunction with these findings, we speculate that listening to music has the potential to alter brain network connectivity organization and that music preference dictates the connectivity that can be expected. While our results almost certainly have developmental and educational implications⁵², more research needs to be performed in these areas before strong conclusions can be made.

It has been shown that the hippocampus is critical in the formation of social and emotional memories⁵³. Our finding that the auditory cortex and hippocampus shared the same module when listening to liked and disliked music supports this implication. Recent results of Burunat et al. relate hippocampal connectivity with working memory for musical motifs during continuous listening²⁹. Our results show that when listening to one's favorite song, the hippocampus functionally separated from the auditory cortex. Perhaps, when listening to a personal favorite song the brain retrieves, rather than encodes, emotionally-laden autobiographic and episodic memories¹⁵. This is consistent with the notion that when listening to a favorite song or music, memory formation is no longer critical as memories associated with a personal favorite song have been previously encoded. In summation, by combining the two community structure findings, our results suggest that listening to a favorite song has the potential to

not only recruit those previously encoded memories but also, even more importantly, to simultaneously support and sustain brain introspection via connectivity within the DMN, thus effectively re-processing autobiographic and episodic memories. Again, of interest to us was that this occurred regardless of the type of music and the presence or absence of lyrics.

Combining the DMN and auditory/hippocampus findings, these results also suggest that listening to music that is Liked provides for the possibility of encoding new memories that are associated with prior self-referenced thoughts and memories. In contrast, when listening to the Favorite song, the encoding appears no longer necessary, and circuitry supporting self-referential thoughts within the DMN is dominant. This is in direct contrast to the Disliked condition when the hippocampus was engaged with auditory cortex but the default mode network was disengaged. These findings may have implications for neurological challenges, such as autism, and neurodegenerative disorders, such as Alzheimer's disease^{43,54}, as well as for human development and learning in education³³. Clearly, optimal manipulation of the auditory-hippocampus network as well as the DMN could have important implications for complex neurological disorders and neurorehabilitation.

Conclusion

We have shown that brain network connectivity patterns are associated with music listening and preference. These current findings indicate that regardless of the acoustical characteristic, functional brain connectivity states depend on whether the music is liked, disliked, or a favorite song. Listening to music that is liked or a favorite song affects functional connectivity in regions involved in self-referential thought and memory encoding, such as the default mode network and the hippocampus. While perhaps everyone intuitively understands the mental experience or feeling when listening to his or her preferred music, whether it is Beethoven's 9th Symphony or *Les Misérables*, or when listening to their favorite song, such as one from Allison Kraus or Eminem, we show here that this similarity of experience manifests in the brain by engaging the DMN. As the first study to apply network science methods to 'real-world' music listening, these results provide a glimpse into the neural patterns underlying the emotion-cognitive states associated with listening to preferred and favorite music.

Methods

Participants. All methods were carried out in accordance with the approved guidelines from the Wake Forest University Medical Center Institutional Review Board. Participants were recruited by flyer and word of mouth and signed Informed Consent documents and experimental protocols approved by the Wake Forest Baptist



Medical Center Institutional Review Board. We recruited 21 young adults (average age 24 ± 3.4 yrs; 13 female) based on their most preferred musical genre: classical ($n = 5$), country ($n = 5$), rap/hip hop ($n = 5$), and rock music ($n = 6$). The genre-ranking of the 11 genres before enrollment in the study was used to ensure we did not bias the study toward participants who only liked a certain genre. All participants were right-handed, English speaking, color-sighted, had normal hearing and were free from neurological disorders. Prior to scanning, participants completed a comprehensive questionnaire about formal musical training and a genre preference ranking of a total of eleven music genres (classical, country, gospel/blues, rap/hip hop, alternative, rock, Christian, folk, pop, metal, Broadway, jazz, classic rock). Prior to the scanning session, participants were asked to self-report a title of their most favorite song. Participants were instructed that their favorite song did not need to be specifically from their preferred music listening genre, merely that it was their favorite song. Participants provided the title of their favorite song to the experimenter prior to the scanning session. The favorite song was intentionally requested in order to analyze the functional brain connectivity responses separately from their preferred and non-preferred music.

The rationale for choosing to differentiate between overall preferred music and a favorite song was to determine if brain network responses might differ between the two. To clarify further, preferred music is a more broadly experienced musical listening phenomenon that can be envisioned as a preferred music listening overall experience, such as through on-line preferential music listening application streams such as Pandora or Groove Shark. On the other hand, and often in contradiction to one's overall musical listening preferences, an individual's all-time favorite song may not coincide with an individual's preferred genre. Indeed, in this study, there were many of our participants who reported a favorite song that was outside of their most preferred music listening genre. For example, one of our participant's preferred music was classical music but their self-reported favorite song was a country song by Garth Brooks, a country music singer and artist. Each participant's favorite song title and any other recording specifics, such as the specific artist, conductor and/or year of performance, was provided to the experimenter prior to the participant's scanning session. Ten subjects reported having formal musical training. Eight had completed, or were in the process of completing, a university music degree. Eleven reported that they could read music fluently. For the favorite song, participants were simply to self-report and provide a title to their favorite song by being asked, "I want the name of your favorite song, the one that, 'Rocks your world', 'Floats your boat', and 'You love this song'". Further details, including the pre-reported favorite songs, are contained in the Supporting Information.

Stimuli. Six musical selections, hereafter referred to as songs, were presented pseudo-randomly to each participant in the MRI scanner while blood oxygen level dependent (BOLD) functional MRI (fMRI) data were collected. The six songs, each five minutes long, included four pre-selected songs considered iconic within each musical genre, an unfamiliar selection, and a sixth personal favorite song. The five songs presented to every subject were Movement I from Symphony No. 5 by Beethoven (classical genre), "Water" by Brad Paisley (country genre), "OMG" by Usher (rap/hip hop genre), "Rock 'N Roll All Nite" by KISS (rock genre), and "Spring Hall" by the Chinese Jinna Opera Band (unfamiliar genre). Favorite songs ranged from Rhinoceros & Eminem to Rachmaninov (for the list of favorite songs see Supporting Information).

Scanning Procedures. Prior to the scan session, participants were trained to use a Visual Analog Scale (VAS) to rate how much they liked/disliked each song selection. With this procedure, we were able measure subjective preference across participants⁵⁴. During the scanning procedure each participant listened to six musical selections. Each selection was presented as a continuous audio clip of five minutes with no interruptions. The music genre clips included rock, rap, classical, country, an unfamiliar piece, and their pre-reported favorite song. Before the onset of imaging and with the scanner on, participants had their headphones tested and the music volume adjusted. Prior to presentation of the musical selections, a five minute eyes-closed at-rest scan was acquired. During the entire musical portion of the scanning procedure, all participants had their eyes closed. Unbeknownst to the participants, songs were played for each participant in a randomized order based on an overarching scheme by genre preference from a pre-study music genre preference questionnaire. However, because the music preference questionnaire included rating scale choices of a total of eleven (11) genres, the 4 genre songs appeared as randomly presented to the participants. Each participant provided the title of their self-determined favorite song that was presented last. Participants rated their preference for each song from 1–10 using the visual analog scale (VAS) when each selection ended and before the next song was presented. The highest VAS score report was used to determine their top preferred music during the scanning session. The lowest VAS score was used to determine their least preferred music during the session. The favorite song, the title of which was provided by each participant to the experimenter during the screening session, was presented last. See Supporting Information for a discussion of possible ordering effects associated with the song presentation order.

MR scans were performed on a 1.5 T GE twin-speed LX scanner with birdcage 12-channel head coil (GE Medical Systems, Milwaukee, WI). For blood oxygenation level-dependent (BOLD) contrast, T2*-weighted functional images were acquired using a single-shot, gradient-recalled, echo-planar imaging sequence: TR/TE = 2000/40 ms, voxel size $3.75 \times 3.75 \times 5$ mm³. To allow for all songs to be played in their entirety, songs were edited for a total continuous playing time of five minutes. 150 brain volumes were collected per MRI run, and the first 6 volumes were not included

in the network analyses, as this was the time during which the BOLD signal achieved steady-state.

Network Generation and Analysis. Network generation and analysis was performed using the fMRI time series data from each subject with eyes closed. Acquired images were motion corrected, spatially normalized to the MNI (Montreal Neurological Institute) space, and re-sliced to $4 \times 4 \times 5$ mm³ voxel size with an in-house processing script using FSL package (FMRIB-University of Oxford). Imaging data was filtered (0.00945–0.084 Hz) and head motion (6 rigid-body transformation parameters) and mean signal (whole-brain, white matter, and ventricles) were regressed from the data to limit effects due to physiological noise^{55–57}. Networks were then generated using a Pearson correlation with each voxel (~21,000) representing a network node. This produced a cross-correlation matrix containing the Pearson correlation coefficient representing the strength of association between each voxel pair.

The correlation matrix was then thresholded to generate a sparse network in keeping with other biological networks⁵⁸. The threshold was based on a relationship between the number of nodes and the average node degree (K). This procedure ensured that comparisons across subjects were based on networks with comparable densities. Details of the thresholding procedure and the rationale for the chosen threshold are presented in the Supporting Information. Briefly, the threshold is based on $S = \log(N)/\log(K)$. For the data presented here, a threshold of $S = 2.5$ was applied to the matrix, resulting in the binary adjacency matrix (A_{ij}). Once the complete adjacency matrix was generated for each subject, network statistics were calculated. The network statistics for each node were mapped back into 3D brain space to identify the spatial location of key network nodes and network communities. Networks were generated for each participant using the fMRI time series from each subject's six musical experiences. Results presented here are from the participants' favorite song and the highest and lowest rated songs from the five experimenter-selected genres. Therefore, we conducted three separate network calculations based on most and least preferred songs of the iconic music selections and one for their personal favorite song.

Network Properties. The analyses focused on four network properties: degree, global efficiency, local efficiency, and community structure. Degree (K) is the number of edges or *functional links* for an individual node. Global efficiency (Eglob) is a measure of the distance (in network space) from a given node to every other node in the network⁵⁹. Eglob is calculated as the average of the inverse of the shortest paths between node i and all other nodes in the network. This property is scaled ranging from 0 (indicating no path between nodes) to 1 (direct connection between nodes). Disparate regions of the brain can have high global efficiency if the path length for nodal communication is sufficiently short. Local efficiency (Eloc) is a measure of local neighborhood connectivity. Eloc is calculated by computing the global efficiency of a sub-graph of node i . In other words it measures the distance between all the neighbors of node i . This statistic also ranges between 0–1, with larger values indicating that the neighbors of a particular node are highly connected to each other. A detailed description of the properties calculated in this study may be found in multiple review articles^{20,21,55}. Once network statistics were calculated, we evaluated the location within the brain of the nodes with the highest statistics. Visual depictions of network maps in brain space focused on "network hubs" heuristically defined as the top 20% of the nodes for each of the network statistics. Statistical analyses were performed by comparing the actual network statistics, with no arbitrary threshold, within specific regions-of-interest (ROIs) located in the precuneus and in the auditory cortex. The precuneus ROI was a 12 mm sphere centered at 0, -54, 34 in MNI space. The auditory ROI consisted of bilateral boxes (16 mm \times 16 mm \times 10 mm) centered at 54, -12, 2 and -52, -12, 2 in MNI space.

Community Structure. Community structure is a multivariate analysis that identifies collections of network nodes that are more interconnected with each other than they are with other network communities. The analysis used was based on modularity (Q) introduced by Newman and Girvan⁶⁰. Details of the community structure analyses are presented in the Supporting Information. Briefly, hierarchical network partitioning was performed using the algorithm called QCut developed by Ruan and Zhang⁶¹. The optimal partition was identified using Q and was the basis of all further analyses. Due to the multivariate nature of community structure, it is not possible to simply identify a representative module for a group of individuals. However, scaled inclusivity (SI) is a statistic that can be used to determine the consistency of a given network community across individuals⁶². This analysis was used to evaluate the consistency of the community encompassing the precuneus and the community encompassing the auditory cortex under the three conditions (for detailed information see Supporting Information).

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Author contributions

R.W. conceived and conducted the experiment. R.W. and M.S. processed the data. R.W. and P.L. analyzed the data. R.W. and P.L. wrote the manuscript. R.W., P.L. and J.B. wrote the supplemental manuscript. P.L., D.H. and J.B. acted in an advisory and editorial capacity.

Additional information

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Due to a technical error, the corresponding author is incorrectly given as J. H. Burdette rather than R. W. Wilkins in the HTML version of this Article. For correspondence and requests for materials, please contact R. W. Wilkins (robinwwilkins@gmail.com). This error has now been updated in the original Article.

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